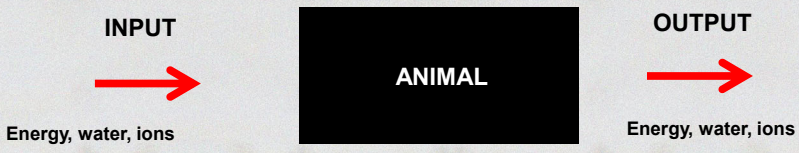
ENVIRONMENTAL PHYSIOLOGY:

- How do animals work in their environment?
- What animals to study?
- Adaptation – Exaptation?
- Adaptations in a phylogenetic context?
- How and why to compare species?
- Phenotype

1

How do animals work?

- Animals are (in a sense) complex machines
- They cannot violate physical/chemical laws
- The black-box approach



2

Studying physiological processes

Nikolaas Tinbergen's four questions

Mechanism Development	Proximate / How
Phylogeny Evolution	Ultimate / Why

Constraints!

3

What animals to study?

- The "August Krogh Principle" or the "champion animal" Walter Heiligenberg
- For any particular questions, pick the animal that best expresses a certain trait / ability / feature as your study animal
- e.g. study desert rodents for kidney adaptations that minimise water loss,
  Hearing in barn owls,
  Vision in raptors, etc

August Krogh: the "grandfather" of comparative physiology

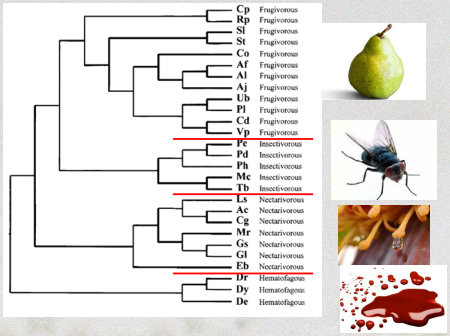
https://jeb.biologists.org/content/217/10/1640

Krogh, A. (1929). The progress of physiology. Am. J. Physiol. **90**, 243-251.

4

Adaptations in a phylogenetic context

- What is the phylogenetic pattern?
- What is the effect of phylogeny on the question?
- What if phylogeny is confounded with other factors? …… the BMR of bats problem.



5

Adaptation

Adaptation can have different meanings in different contexts

- Noun: an adaptation e.g. crypic colouration
- A genetic process: whereby an animal becomes genetically adapted to its environment by natural selection
- A plastic process of change: whereby an animal responds to environmental change
  - by acclimation (in the laboratory)
  - or acclimatisation (in the field)

6

Noun: Adaptation

- An adaptation is a feature produced by **natural selection for its current function.**
- Based on this definition, we can make specific predictions ("If X is an adaptation for a particular function, then we'd predict that...") and see if our predictions match our observations.

7

Adaptations can seem self-evident

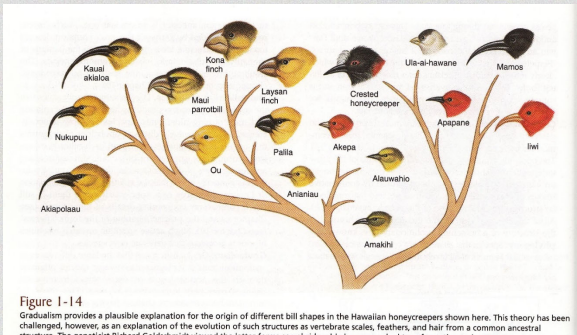


Figure 1-14
Gradualism provides a plausible explanation for the origin of different bill shapes in the Hawaiian honeycreepers shown here. This theory has been challenged, however, as an explanation of the evolution of such structures as vertebrate scales, feathers, and hair from a common ancestral structure. The geneticist Richard Goldschmidt viewed the latter forms as unbridgeable by any gradual transformation series.

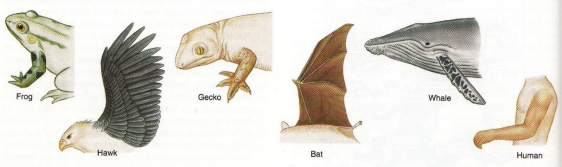


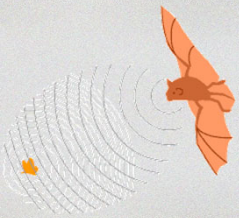
Figure 1-15
According to Darwinian evolutionary theory, the different forms of these vertebrate forelimbs were molded by natural selection to adapt them for different functions. We show in later chapters that, despite these adaptive differences, these limbs share basic structural similarities.

8

Adaptation *vs* Exaptation

Adaptation—a feature produced by natural selection for its **current** function.

Exaptation—a feature that performs a function but that did not result from natural selection **for its current use**. Perhaps the feature was produced by natural selection for a function other than the one it currently performs and was then co-opted for its current function.



For example:

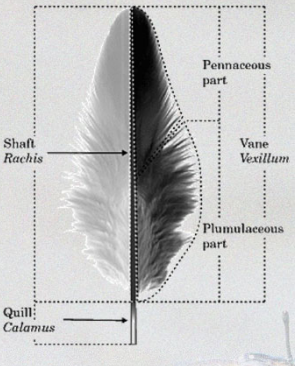
- did bat echolocation evolve for feeding or navigation? Is one function an adaptation and one an exaptation?
- bird feathers might have originally arisen in the context of selection for insulation or feeding, and only later were they co-opted for flight. In this case, the feather is an adaptation for endothermy and an exaptation for flight.

9

Are feathers an adaptation for bird flight

Is the evidence consistent with this hypothesis?

1. Heritable?
2. Functional?
3. Adaptive?
4. Current Function?



10

1. Heritable?

- If it has been shaped by natural selection, then it must be genetically encoded—since natural selection cannot act on traits that aren't passed on to offspring.

Are feathers heritable?

- Yes. Baby birds grow up to have feathers like those of their parents.

11

2. Functional?

If it has been shaped by natural selection for a particular task, then the trait must actually perform that task.

Do feathers function to enable flight?

- In the case of bird flight, the answer is fairly obvious. Birds with feathers are able to fly and birds without feathers would not be able to.

12

3. Adaptive?

If it has been shaped by natural selection, an adaptation must increase the fitness of the organisms that have it—since natural selection only increases the frequency of traits that increase fitness.

Are birds with feathers more fit than birds without?

Birds without feathers aren't going to leave as many offspring as those with feathers. (BUT, has anyone done the experiment??!!)

13

4. Current Function

Did the trait arise for the current function? Did feathers appear when flying evolved?

- The answer is probably no. The closest fossil relatives of birds, two-legged dinosaurs called theropods, had feathers but could not fly.
- Thermoregulation?
  Communication?
- Feeding?

14

Feathers are an exaptation for flight

So, feathers may be an **exaptation** for flight and an **adaptation** for some other original function (thermoregulation, communication or feeding).

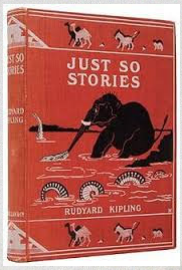
Considering questions like these has led biologists to look for alternate scenarios for the initial evolution of feathers.

So bird feathers are not an adaptation for flight, but most likely the shape of the feathers are.

15

Is Everything Adaptive/Exaptive?

- Although living animals have some amazing adaptations, many characteristics of species are possibly not adaptations or exaptations at all.
- It's tempting to look for adaptative explanations for everything.
- We can make up a "just so" story, but there are other explanations to consider.



16

The result of history/chance – genetic drift

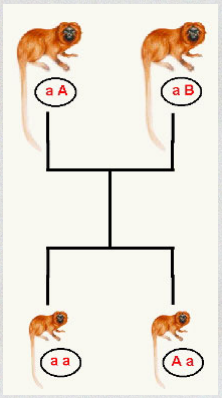
Why does the base sequence GGC code for the amino acid glycine in a protein, as opposed to some other amino acid?

How much variation is maintained/lost through genetic drift?

In this example, the parents carry three different genes for a particular trait: a, A and B. By chance, here they pass on only a and A to their offspring. Gene B is lost due to random chance.

In this example, on average:

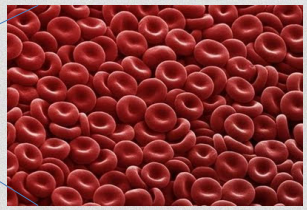
- a will be lost 6% (6.25%) of the time (0.5^4)
- A will be lost 25% of the time
- B will be lost 25% of the time



17

Just a by-product

Why is blood red?
It's colour is a by-product of the chemistry of blood, which causes it to reflect red light/absorb blue light. The chemistry of blood may be an adaptation, but blood's redness is not itself an adaptation



(except maybe as an exaptation for a few animals e.g. eye-blood squirting lizards).

18

An outdated adaptation

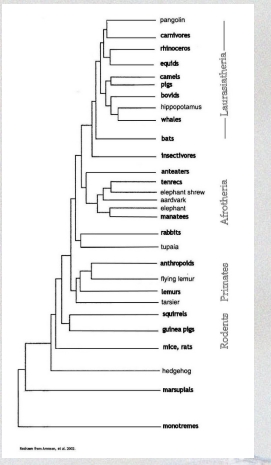
It might have been an adaptation in the past but not the current environment.

For example, the large, hard-shelled fruit of the calabash tree is actually an adaptation for seed distribution by large mammals such as gomphotheres. But these early relatives of elephants went extinct over 10,000 years ago! If this hypothesis is correct, then these fruit characteristics can no longer be considered adaptive for seed distribution. They may even now be maladaptive!

19

Why a comparative approach? And how to compare species?

- Common themes across species/taxa provide insights
  → Convergence – Divergence patterns
  It is often the only way we can distinguish between Adaptation, exaptation, and random outcomes
- Non-Independence of Species
- Comparative Methods
  Phylogenetically-informed Analysis
  (Independent Contrasts)
  (Phylogenetic Least Squares Regression)
  (Autoregression)



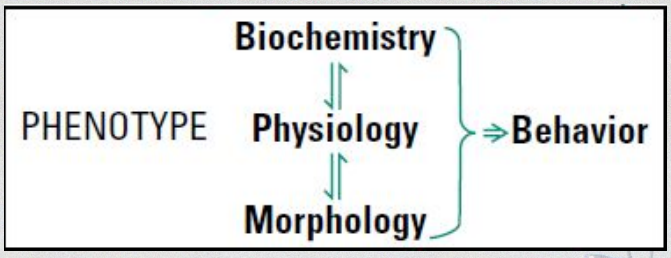
20

Phenotype

Phenotype – what an animal "looks like"

Physiology is one aspect of phenotype, integrated with

- Behaviour
- Biochemistry
- Morphology



21

Adaptation of Phenotype

Phenotype – is adaptive
– how? ……

Genotype – Development – Environment

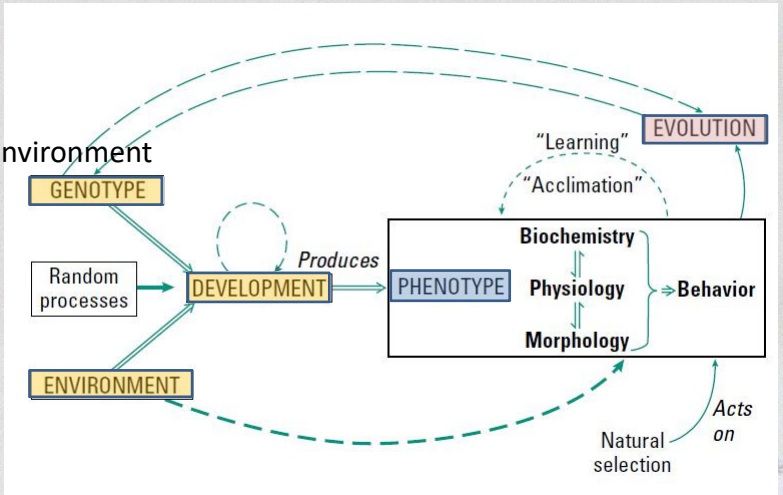


Fig. 1.1

22

Phenotypic plasticity

Effect of environmental change on expression of adult phenotypes

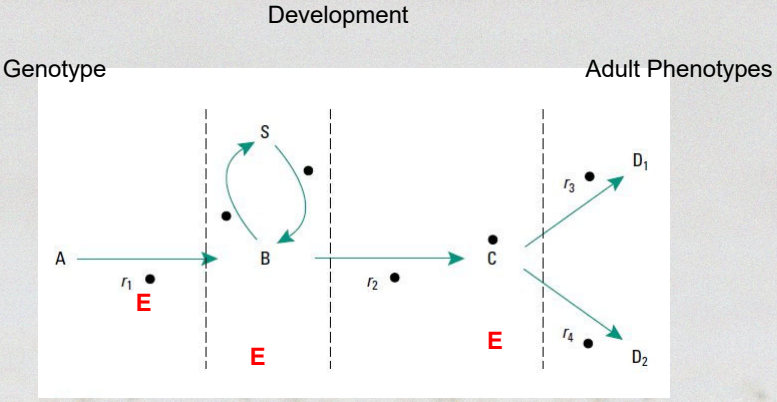
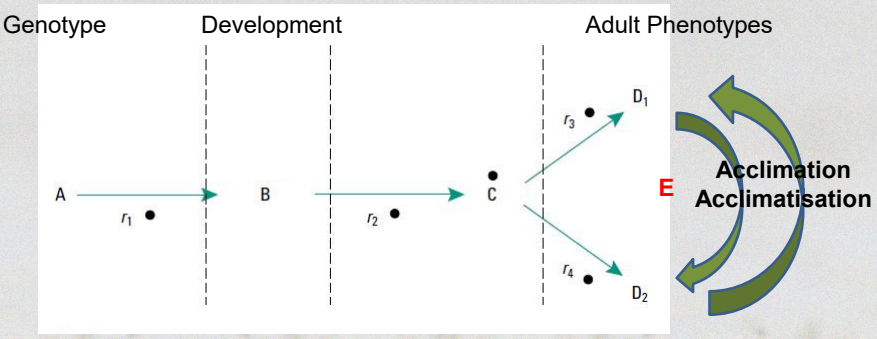


Fig. 1.4

23

Phenotypic plasticity

Effect of environmental change on change between adult phenotypes by
- acclimation (in the laboratory) or
- acclimatisation (in nature)



24